

QUEEN AND FORAGER SIZES OF *BOMBUS AFFINIS* CRESSON  
(HYMENOPTERA: APIDAE)

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*Abstract.*—This study explores the relationships of selected body measurements in the bumble bee *Bombus affinis*, and reviews the literature regarding measuring bumble bees. We found that in foraging workers of this species, collected over 3 sequential years from the same forest sites, compound-eye length, head length, head width, radial-cell length, scapus length, tibia length, and wing length all predicted dry weight, a measure of overall size. These same variables, except for head length, also predicted queen weight. Workers had a higher variance in their radial-cell length than queens, and queens had higher variances in their glossa length and weight than workers. In all 13 regression analyses between body size measurements, worker correlation coefficients ( $r^2$  values) were higher than those for queens. Worker size, measured as head width (a strong predictor of body weight), increased with time during 2 out of 3 flight seasons.

*Key Words:* Apidae, bumble bee, forager size, seasonal size changes, queen size

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Previous studies of *Bombus* size found that the relationships between linear measurements and between linear measurements and weights vary in strength depending on caste, sex, species, and measurement method (Knee and Medler 1965, Morse 1978, Harder 1985, and many references therein). This study on *B. affinis* Cresson examines samples of this bee from the same collection sites for 3 sequential flight seasons, documents many previously unreported intra-individual and forager-queen size relationships in the genus, and discovers an increase in forager size during its flight season.

Sizes of individual *Bombus* affect the pollination ecology of this genus which contains major pollinators in forests, meadows, tundras, and other habitats (Robinson

and Johansen 1978). In some species, larger foragers fly faster, forage more efficiently on certain plants, gather more food during cool weather, obtain food from deeper flowers, and thief less nectar than smaller foragers (Morse 1978, Pyke 1978, Heinrich 1979, Harder 1985). Because males and queens also vary in size within species (Owen 1989), and they are frequent flower visitors, they are also likely to have size-related effects on pollination; however, we found no published studies on this subject.

*Bombus affinis* is a short-tongued bumble bee, found from Ontario to New Brunswick and south to North Carolina (Mitchell 1962). It nests underground and flies from April through October (Laverly and Harder 1988). Wisconsin colonies commonly contain at least 200 workers, and can have up to 350 workers (Medler and Carney 1963).

## MATERIALS AND METHODS

We obtained a total of 475 foragers and 100 queens of *B. affinis* from 29 April through 27 September 1991–1993 with 20 Townes-style Malaise traps in four watersheds in the Fernow Experimental Forest, Tucker County, West Virginia (described in detail in Barrows et al. 1994, Barrows 1995). We emptied the traps every 10 days on the same Julian day of each year. The traps collected the bees in heads with 95% ethanol. We removed bees from alcoholic samples, air dried them for at least 1 yr, and randomly selected specimens for measurements. We then relaxed them in humidity chambers and dissected them to measure their parts.

**Weight.**—We took the weight-1 (W1) and weight-2 (W2) of each bee using an electronic balance (Mettler AE 50). Weight-1 was the weight of a bee's head, mesosoma, and metasoma; W2, the weight of only its head and mesosoma. We took W2s because food and organs within *Bombus* metasomas, e.g., crops, fat bodies, and ovaries, can cause their weights to vary appreciably (Alford 1969, Heinrich 1979). Because some specimens lost parts of their antennae, total antennae, and parts of their legs, we removed their entire antennae and legs distal to their trochanters to control for missing parts, before ascertaining their dry weights.

**Linear measurements.**—We measured left compound-eye length (CL), glossa length (GL), head length (HL), head width (HW), scapus length (SL), and tibia length (TL) using a dissecting microscope with an ocular grid, and we measured forewing lengths (WL1s, WL2s, and WL3s) with a microfiche reader (Minolta RP 605Z). Head width was measured as the greatest distance across a bee's compound eyes; HL, the distance from the vertex to the distal end of her clypeus; GL, the distance from the posterior end of her basiglossal sclerite to the tip of her labellum; WL1, her radial-cell length; WL2, distance from the proximal

end of her median plate to the distal tip of her radial cell; and WL3, the maximum length of her entire forewing.

Before measuring glossae, tibiae, and wings, we straightened glossae by extending them into individual capillary tubes (Harder 1982), removed tibiae from their adjoining femora, and put detached forewings between microscope slides. We used glossae that were either relaxed in a humidity chamber or treated while still attached to their heads in a 10%-KOH solution for 12 hr at 25°C. Wing lengths were measured from images on a microfiche screen (Harder 1982, Owen 1988). Because 11 foragers and four queens had frayed wing tips, we did not attempt to measure their WL3s.

To investigate the change of forager size during the flight season, we measured head widths (HWs) of from one to eight specimens for each sampling period, using a maximum of eight bees when they were available. We measured HW because it is the linear measurement with the highest correlation with weight-2 (W2).

To discover possible correlations between sizes of body parts, we used least-square regression (SPSS for Windows, Norusis 1993). To look for possible differences between measurement variances, we used PROC TTEST (SAS Institute, Inc. 1979).

## RESULTS AND DISCUSSION

Queens of *B. affinis* showed a greater variation in measurement ranges than foraging workers in all measurements, except radial-cell length (WL1) and tibia length (TL) (Table 1). Further, queens had greater variances in glossa length (GL) and weight (W1 and W2) than workers, and the latter showed a greater variance in tibia length (TL) than the former (Table 2). Because queens are larger than workers, they would be expected to show greater variations and variances in all body-part sizes than workers. The possible biological significance of these three surprising exceptions to this expectation awaits discovery.

Workers showed significant correlations

Table 1. Measurements of *Bombus affinis*<sup>a</sup>.

Measurement	Caste	N	Mean $\pm$ 1 SEM, Range (mg or mm)	Range Magnitude	Range Magnitude Queen > Worker
CL	queen	20	3.8 $\pm$ 0.03, 3.5–4.1	0.6	yes
	worker	20	2.7 $\pm$ 0.03, 2.6–3.0	0.4	—
GL	queen	20	6.4 $\pm$ 0.22, 5.4–8.4	3.0	yes
	worker	20	4.3 $\pm$ 0.08, 3.8–5.3	1.5	—
HL	queen	20	5.5 $\pm$ 0.05, 5.1–5.9	0.8	yes
	worker	20	3.8 $\pm$ 0.05, 3.5–4.2	0.7	—
HW	queen	20	5.8 $\pm$ 0.05, 5.1–6.1	1.0	yes
	worker	20	4.2 $\pm$ 0.04, 3.9–4.6	0.7	—
SL	queen	20	2.8 $\pm$ 0.03, 2.5–3.0	0.5	yes
	worker	20	2.0 $\pm$ 0.02, 1.9–2.3	0.4	—
TL	queen	20	6.7 $\pm$ 0.04, 6.5–7.1	0.6	no
	worker	20	4.7 $\pm$ 0.07, 4.2–5.3	0.9	—
W1	queen	20	185.8 $\pm$ 8.51, 129.7–258.8	129.1	yes
	worker	20	58.9 $\pm$ 3.25, 39.0–91.0	52.0	—
W2	queen	20	101.4 $\pm$ 3.56, 74.4–130.5	56.1	yes
	worker	20	34.1 $\pm$ 1.42, 24.0–48.3	24.3	—
WL1	queen	20	4.7 $\pm$ 0.04, 4.3–4.9	0.6	no
	worker	20	3.4 $\pm$ 0.05, 2.9–3.8	0.9	—
WL2	queen	20	14.8 $\pm$ 0.11, 13.9–15.5	1.6	yes
	worker	20	10.8 $\pm$ 0.15, 9.4–11.9	1.5	—
WL3	queen	16	18.3 $\pm$ 0.16, 17.2–19.2	2.0	yes
	worker	9	12.7 $\pm$ 0.18, 11.7–13.2	1.5	—

<sup>a</sup> All measurements are in mm, except for W1 and W2 which are in mg. CL, compound-eye length; GL, glossa length; HL, head length; HW, head width; SL, scapus length; TL, tibia length; W1, combined weight of head, mesosoma, and metasoma without legs and antennae; W2, weight of head and mesosoma without legs and antennae; WL1, length of radial cell of forewing; WL2, the distance from the proximal end of the median plate to the distal tip of the radial cell; WL3, the maximum length of the entire forewing.

( $P \leq 0.05$ ) between all paired variables except for W2 and GL, and queens showed significant correlations between all paired variables except for this same pair and W2 and head length (HL) (Table 3). Worker  $r^2$  values (which indicate the percent of the variability of the dependent variable explained by the independent variable) are higher than those for queens for all paired measurements. This suggests that natural selection has favored less variable body proportions in these foraging workers than in queens, and this is possibly related to greater behavioral specialization in foragers. They build brood cells, care for immatures, find and collect food, and work on and protect nests. Queens, which have greater behavioral versatility than workers, perform the above duties, and in addition, they search for hibernacula and nesting sites, hibernate, and mate.

Researchers have used different morphological features to estimate overall *Bombus* body size. Hobbs et al. (1961) measured their total body lengths, but considered them to be inaccurate reflections of size, due to the compressibility of metasomas. Medler (1962a), Knee and Medler (1965), Plowright and Jay (1968), Harder (1982) and Owen (1988, 1989) measured radial-cell lengths (WL1s). Plowright and Jay (1968) also used head width (HW) as a size indicator. Röseler and Röseler (1974), Morse (1977, 1978), and Harder (1982, 1985) measured wing lengths. However, only a few investigators examined the correlation of linear measures of body parts and weight. Harder (1985) found high, positive correlations between GL and body weight and between wing length and body weight in foragers and queens of seven *Bombus* spp., but he did not indicate exactly

Table 2. Comparisons of measurement variances of queens and workers in *Bombus affinis*<sup>a</sup>.

CL	queen	0.014	worker > queen	0.8276
	worker	0.015		
GL	queen	0.745	queen > worker	0.0007 <sup>b</sup>
	worker	0.115		
HL	queen	0.047	worker > queen	0.9304
	worker	0.049		
HW	queen	0.058	queen > worker	0.3475
	worker	0.038		
SL	queen	0.017	queen > worker	0.2065
	worker	0.010		
TL	queen	0.032	worker > queen	0.0310 <sup>b</sup>
	worker	0.094		
W1	queen	1,447.829	queen > worker	0.0001 <sup>b</sup>
	worker	211.223		
W2	queen	254.116	queen > worker	0.0001 <sup>b</sup>
	worker	39.687		
WL1	queen	0.028	worker > queen	0.1678
	worker	0.053		
WL2	queen	0.218	worker > queen	0.1131
	worker	0.459		
WL3	queen	0.421	queen > worker	0.6130
	worker	0.292		

<sup>a</sup> Abbreviations are the same as in Table 1.

<sup>b</sup>  $P \leq 0.05$ . The null hypothesis is that the worker and queen variances are equal.

how he measured weight. Owen (1988) reported positive correlations between WL1 and body weight in *Bombus* queens of five of his eight investigated species. Neither researcher included *B. affinis*. We found that the highest morphological correlation between a weight and linear measurement in foragers is between W2 and HW ( $r^2 = 0.74$ ) and in queens, between W2 and TL ( $r^2 = 0.55$ ) (Table 3).

In our sample of 20 humidified *B. affinis* foragers, GL correlated with CL ( $r^2 = 0.55$ ,  $P = 0.001$ ), but not with HW ( $r^2 = 0.31$ ), W2 ( $r^2 = 0.20$ ), or WL1 ( $r^2 = 0.24$ ). However, in our sample of 10 KOH-treated bees, GL and HW were correlated ( $r^2 = 0.64$ ,  $P = 0.006$ ), which indicates that the procedure used to relax dry specimens influences GLs.

Alpatov (1929) found the tongues of dry honey bees to be "about 6.5% shorter than the natural." Hobbs et al. (1961) stated that the GL of a dry bumble bee depends on whether it died with its tongue distended or contracted. Medler (1962b) investigated the

correlation of different mouthparts to the WL1 for 14 *Bombus* species, and found them to be positively correlated, except in the queens of four species including *B. affinis*. Morse (1977) and Harder (1982) confirmed these results, and found even higher correlations for their samples, but did not investigate *B. affinis*. Waddington (1987) reported positive correlations between GL, HW, and WL1 in honey bees. Harder (1982) measured GL of specimens preserved in 70% ethanol and mentioned that a bee with its proboscis folded appears to have a shorter tongue than one with its proboscis extended. He suggested that the "sheath's compressibility and the freedom of the glossal rod from the sheath distally, which allows some of the rod to be drawn into the prementum during lapping and folding," accounts for this variability. We observed such GL differences macroscopically in *Bombus affinis*.

We found that W1 and W2 were correlated with one another in both queens and foragers of *B. affinis*. This indicates that

Table 3. Measurement regressions of *Bombus affinis*<sup>a</sup>.

Regression	Caste	r <sup>2</sup>	P	Regression Equation
W1 vs. W2	queen	0.81	0.0001 <sup>b</sup>	W1 = -32.307 + 2.149 (W2)
	worker	0.88	0.0001 <sup>b</sup>	W1 = -14.868 + 2.165 (W2)
W2 vs. CL	queen	0.25	0.0245 <sup>b</sup>	W2 = -159.620 - 68.504 (CL)
	worker	0.68	0.0001 <sup>b</sup>	W2 = -81.140 + 42.429 (CL)
W2 vs. GL	queen	0.01	0.7269	W2 = 89.801 + 1.947 (GL)
	worker	0.19	0.0800	W2 = 1.323 + 7.878 (GL)
W2 vs. HL	queen	0.17	0.0704	W2 = -67.295 + 30.419 (HL)
	worker	0.45	0.0011 <sup>b</sup>	W2 = -38.360 + 19.221 (HL)
W2 vs. HW	queen	0.40	0.0030 <sup>b</sup>	W2 = -140.141 + 41.534 (HW)
	worker	0.74	0.0001 <sup>b</sup>	W2 = -83.866 + 28.001 (HW)
W2 vs. SL	queen	0.33	0.0085 <sup>b</sup>	W2 = -95.292 + 69.129 (SL)
	worker	0.50	0.0005 <sup>b</sup>	W2 = -57.711 + 45.402 (SL)
W2 vs. TL	queen	0.55	0.0004 <sup>b</sup>	W2 = -320.748 + 62.512 (TL)
	worker	0.62	0.0001 <sup>b</sup>	W2 = -42.532 + 16.175 (TL)
W2 vs. WL1	queen	0.32	0.0096 <sup>b</sup>	W2 = -152.211 + 53.976 (WL1)
	worker	0.66	0.0001 <sup>b</sup>	W2 = -42.036 + 22.301 (WL1)
W2 vs. WL2	queen	0.38	0.0038 <sup>b</sup>	W2 = -211.339 + 21.043 (WL2)
	worker	0.69	0.0001 <sup>b</sup>	W2 = -49.339 + 7.705 (WL2)
W2 vs. WL3	queen	0.46	0.0037 <sup>b</sup>	W2 = -230.044 + 18.188 (WL3)
	worker	0.48	0.0384 <sup>b</sup>	W2 = -52.032 - 6.552 (WL3)
WL1 vs. HW	queen	0.53	0.0003 <sup>b</sup>	WL1 = 1.787 + 0.504 (HW)
	worker	0.70	0.0001 <sup>b</sup>	WL1 = -0.783 + 0.996 (HW)
WL2 vs. WL1	queen	0.91	0.0001 <sup>b</sup>	WL2 = 2.325 + 2.668 (WL1)
	worker	0.95	0.0001 <sup>b</sup>	WL2 = 1.021 + 2.873 (WL1)
WL3 vs. WL1	queen	0.84	0.0001 <sup>b</sup>	WL3 = -0.073 + 3.884 (WL1)
	worker	0.93	0.0001 <sup>b</sup>	WL3 = 2.305 + 3.166 (WL1)

<sup>a</sup> The abbreviations are the same as in Table 1.

<sup>b</sup>  $P \leq 0.05$ .

dried objects in metasomas did not weigh enough to obscure these correlations under our study conditions.

Nonetheless, internal food, stored-fat, and ovarian development can affect a fresh bumble bee's overall weight. A bumble bee can become up to 100% heavier due to provisions in its honey crop found in its metasoma (Heinrich 1979). Researchers have measured fresh *Bombus* body weight, but they either ignored internal food (Pyke 1978), or tried to account for it by starving the bees for 12 to 18 h before weighing them (Harder 1983, 1985, Owen 1988). According to Alford (1969), fat makes up an average of 34% of the total dry weight of queens in autumn. Fat and glycogen are stored in the fat body, located in the metasoma. Holm (1972) reported an average fat content of 21% in the dry matter in the me-

tasoma of autumn queens and 12% in spring ones. Because most of the queens investigated in our study were spring queens, fat may have made little contribution to their weight variability. Finally, ovarian developmental state contributes to the varying weight, especially in queens caught in spring (Cumber 1949).

In *B. affinis*, measurements of foraging worker HWs within a season indicate that forager size increased in 1992 ( $r^2 = 0.93$ ;  $P < 0.001$ ;  $N = 52$ ) and 1993 ( $r^2 = 0.61$ ;  $P = 0.005$ ;  $N = 64$ ), but not in 1991 ( $r^2 = 0.02$ ;  $P = 0.734$ ;  $N = 33$ ) (Fig. 1). The small 1991 sample size possibly prevented our finding a forager size increase for that year.

Worker size might increase during flight seasons in many *Bombus* species. So far, quantitative studies have also documented

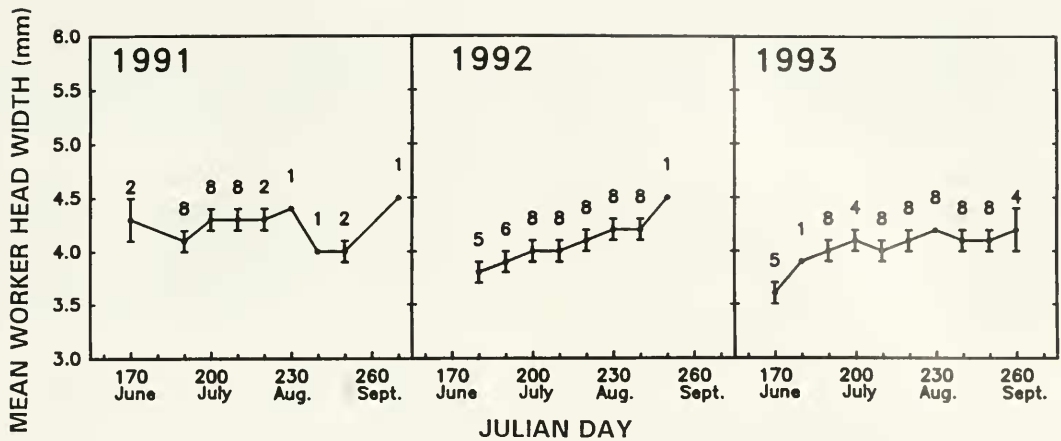


Fig. 1. Mean worker head width versus sampling period, Fernow Experimental Forest, WV, 1991–1993.

this increase in *B. fervidus* (Fabricius), *B. griseocollis* (De Geer), *B. nevadensis auricomus* (Robertson), and *B. perplexus* Cresson (Knee and Medler 1965, Plowright and Jay 1968). These increases occurred in healthy bumble-bee colonies, but the size of workers decreased when colonies were parasitized (Knee and Medler 1965). Our samples from Malaise traps may have contained bees from both healthy and parasitized colonies, and colonies in different developmental stages, which might have lowered our size-season correlation coefficients.

In conclusion, we found that many body measurements are significantly correlated with body weight and other body measurements in both queens and foraging workers of *B. affinis*. Tibia length is most correlated with weight in queens, and head width is most correlated with weight in workers. Radial-cell length is highly correlated with total wing length in both castes. Laboratory-preparation methods influenced glossa length, and, therefore, whether it correlated with other body parts in our study. Forager size increased during the flight season in 2 out of 3 yr. Our results and literature review suggest that researchers should measure other *Bombus* species from different habitats to obtain a more complete understanding of *Bombus* size. Further, the relationships of queen and worker size with com-

petitive interactions involving conspecific bees and other animals at flowers, foraging efficiency, frequency of flower robbing and thieving, kinds of flowers used, and other phenomena still remain unstudied, or only meagerly studied, in most *Bombus* species.

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